

THE DEVELOPMENT OF MARINE FOULING COMMUNITIES

BRADLEY T. SCHEER

Wm. G. Kerckhoff Marine Laboratory, California Institute of Technology, Corona del Mar

This paper constitutes an examination of the sedentary communities found on float bottoms and other submerged objects in Newport Harbor, California. Particular attention has been paid to the changes in composition of such communities with time.

The basic problem in the development of a sequence of communities in a limited environment is that of distinguishing between seasonal progression and true succession. Seasonal progression results fundamentally from differences in breeding seasons of various organisms. This type of development was noted at Beaufort, N. C. by McDougall (1943). Most of the organisms observed by McDougall had short life cycles and short breeding seasons. As a result, most of the organisms which settled in the winter months were dead or moribund by spring, and were replaced by organisms breeding in the latter season.

Succession, in contrast to seasonal progression, involves definite relations between organisms. Shelford (1930) has suggested the following criteria for the occurrence of succession: (1) Early forms must drop out, and be replaced by later forms, and (2) Some of the earlier forms must be essential for the establishment of the later forms. The use of the word "essential" in this connection is perhaps unfortunate. It would be nearly impossible, in most cases, to prove that one organism is essential for the establishment of another. On the other hand, the presence of one organism might well provide conditions favoring the establishment of another, and certainly such favorable conditions would suffice to insure the displacement of early settlers by later arrivals.

The phenomena of ecological succession are well known in terrestrial communities. In littoral marine communities, it has sometimes been stated that true succession does not occur, or is of little importance (Shelford, 1930; McDougall, 1943). The clearest case of succession in intertidal communities is that reported by Hewatt (1935). In the *Mytilus californianus* community characteristic of exposed rocky coasts along the entire Pacific coast of the United States, the establishment of a climactic condition requires more than two and one-half years, and involves a definite sequence of organisms. The reports of Kitching (1937), Moore (1939) and Moore and Sproston (1940) also give some indication that recolonization of intertidal rock surfaces is a slow process. It appears that the first event is ordinarily a heavy settlement of algae, and that many animal forms appear only after the plants have become established. Kitching (1937) provides evidence of a succession of algal forms on rocky intertidal ledges.

The sedentary organisms inhabiting floats, pilings, boat bottoms and similar structures have been the subject of many investigations. The literature in this field has been reviewed recently by McDougall (1943) and need not be cited ex-

tensively here. The most thorough investigations dealing with the Pacific forms are those of Coe (1932) and Coe and Allen (1937). These studies, covering a period of nine years, have provided invaluable information regarding the biology of the organisms concerned. The data reported in the current study have been accumulated between February 1943 and March 1945.

THE FLOAT-BOTTOM COMMUNITIES OF NEWPORT HARBOR

Field observations on float bottoms and similar structures in Newport Harbor disclosed the existence of five or six rather definite communities. For convenience, throughout this paper, these communities will be referred to by designations indicating the most abundant organisms in the community. In this way, we may designate (a) algal, (b) bryozoan, (c) *Ciona*, (d) *Styela*, (e) *Mytilus*, and (f) *Balanus* communities. These communities were not all sharply marked off, one from another, and communities intermediate in composition between algal and bryozoan, bryozoan and *Styela*, *Styela* and *Mytilus*, bryozoan and *Mytilus*, and *Ciona* and *Mytilus* have been observed. The various communities showed no relation to the position of the floats in the harbor, and indeed several different communities were found within a distance of a hundred feet on different floats. Evidence will be presented that this results from a definite succession, and that the composition of the community on any particular float bottom depends on (a) the length of time during which the float has been in the water, and in part on (b) the season during which the float was first immersed. We shall first consider the composition of the various communities.

The bottoms of floats were examined with the aid of a periscopic device involving an ordinary underwater viewing glass with a mirror attached (Fig. 1). Organisms were also removed from floats with a long-handled scraper.

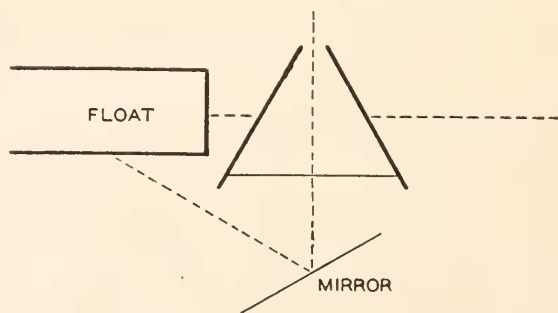


FIGURE 1. Apparatus for the examination of float bottoms.

The algal community. When a clean surface was placed in the bay, the first settlers were bacteria, algae, protozoans, and, during the cooler months of the year, hydroids. The algae included small sedentary diatoms which have not been identified in the present study (see Coe, 1932; and Coe and Allen, 1937), colonial diatoms of the genus *Licmophora*, and one or more species of *Ectocarpus*, notably *E. granulosoides*. In addition, *Enteromorpha* sp., *Lophosiphonia villum*, and *Pterosiphonia bipinnata* were frequently noted. The sedentary protozoans in-

cluded a form similar to *Zoothamnium*, and the suctorian *Ephelota*. There were seven or eight species of hydroids; these were not identified, but *Obelia dichotoma* was usually conspicuous. Bryozoans were found in this community, sometimes in abundance. On float bottoms, *Bugula neritina* may be an important member of the community, and *Membranipora tuberculata* was observed in one instance on glass plates. *Eucratea clavata*, a small semi-erect bryozoan, occasionally occurred in considerable numbers on glass plates. Finally, young colonies of a number of other species of bryozoans appeared after a time. These will be discussed in more detail later.

The bryozoan community. A good many floats supported a very heavy growth of bryozoans. The principal organisms involved were the encrusting bryozoans *Schizoporella unicornis*, *Cryptosula pallasiana*, *Rhynchozoon tumulosum* and *Holoporella aperta*. The erect bryozoans were less constant in occurrence, but were quite abundant in some cases. *Bugula neritina* was less frequent in this community than among the algae, while *Eucratea clavata* was more frequently found among the encrusting bryozoans than among the algae. *Crisulipora occidentalis* and *Scrupocellaria diegensis* were usually present and often very abundant among the bryozoans. Four or five other species of erect bryozoans occurred less frequently.

Although the bryozoans by far outnumbered the other members of this community in most cases (Table VII), other organisms were often quite abundant. Notable are the serpulid worm *Eupomatus gracilis*, and the colonial amphipod *Erichthonius brasiliensis*. *Eupomatus* was almost always found, with its winding calcareous tubes, between the colonies of encrusting bryozoans. Occasionally, it was very abundant, the tubes making a more or less solid mass. *Erichthonius* was irregular in occurrence. During 1943, it did not appear in quantity, but in 1944 it was extremely abundant during July and August, the mud tubes often covering as much as half of the area of a glass plate. Coe and Allen (1937) noted a similar variation at La Jolla. The ascidians *Styela barnharti*, *Halocynthia johnsoni*, and *Ciona intestinalis*, and the mussel *Mytilus* sp. were found among the bryozoans in many cases, but since they were more characteristic of other communities, they will be dealt with later. Many crustaceans, annelids and other motile forms used the bryozoan clumps for shelter.

The Ciona community. The previous paragraphs have dealt with communities in which several species were abundant and the proportions of each species showed considerable variation in different communities of the same type. Most of the *Ciona* communities, in contrast, were composed almost wholly of specimens of *Ciona intestinalis*. This was particularly true during the summer and fall, when these communities were at their peak of development. Many float bottoms presented a solid mass of *Ciona*, with only a few other organisms present. These latter were usually colonial ascidians, growing on the tests of the *Ciona*, and such crustaceans and annelids as might have taken refuge among the stalks.

The Styela community. This was a poorly defined community, intermediate in composition between the bryozoan and *Mytilus* communities. The encrusting bryozoans noted earlier were usually present, forming a substratum for the stalks of *Styela*, while the erect bryozoans were often found among these stalks. Small specimens of *Mytilus* were often attached to the stalks in large numbers. Large

sponges, which have not been identified, were also frequently present, sometimes in such quantity as to dominate the community. It might indeed be preferable to refer to a *Styela*-Sponge community.

The Mytilus community. *Mytilus* was without question the most abundant dominant on the float bottoms in Newport Bay during the period of this study. This has not always been the case, according to reliable observers (G. E. MacGinitie, A. M. Strong, personal communications); during several previous years, *Mytilus* has not been abundant in the bay. The exact identity of this mussel remains in doubt. It is probably the same form which has been recorded infrequently from this area as *M. edulis*. However, conchologists are not entirely agreed that this is the proper designation. It is certainly not *M. californianus*. The *Mytilus* communities sometimes were observed on a substratum of old and badly decayed bryozoans; at other times they were attached directly to the float bottom. Old specimens of *Styela* or *Ciona* were often present among the mussel clumps, and various types of sponge were often quite abundant.

The Balanus community. Communities in which *Balanus* is the dominant organism were not observed on float bottoms in Newport Harbor, although they are frequently observed on experimental surfaces exposed in the open sea at La Jolla. Indeed, *Balanus tintinnabulum* is probably the principal dominant at La Jolla (Coe, 1932). One experimental panel exposed at this laboratory developed a *Balanus* community comparable to those observed at La Jolla, however.

CHANGES IN FLOAT-BOTTOM COMMUNITIES

Eight floats, all located along the mainland side of the channel between Balboa Island and Corona del Mar, and within a distance of 100 yards of one another, were selected in September of 1944, and kept under observation for a period of six months. The results of this study are presented in Table I. At intervals of about one month, the bottom of each float was examined with the viewing glass, and samples of the population removed by hand and with the scraper for later examination in the laboratory.

Float number one had been immersed in the bay for only about one week previous to the first examination. It had at that time (Sept. 21) a typical algal community, with a few specimens of *Bugula*. In October, examination showed increased numbers of *Bugula*, and a few small colonies of other erect bryozoans. In November, *Bugula* and the encrusting bryozoan *Holoporella* had displaced the algae, and a number of small specimens of *Ciona* were present. The float was then covered with a typical bryozoan community. During the remainder of the period, until March, the encrusting bryozoans continued to increase in numbers and size.

Floats 2 and 3 supported typical bryozoan communities in September. In addition to the bryozoans, a number of specimens of *Ciona* were observed, and several small *Mytilus*. During the period of observation, *Mytilus* grew at the expense of the bryozoans and ascidians, becoming very abundant in December, and largely dominating the community by February. The two float populations were very similar in composition in September, but the presence of *Styela* on float 3 in October appears to have favored the earlier establishment of *Mytilus* on this float. The presence of sponges on this float may also be related to *Styela*. Float 4, in Sep-

TABLE I
Changes in composition of float-bottom populations, September 1944 to March 1945

| Float number | September 21, 1944 | October 23, 1944 | November 22, 1944 | December 21, 1944 | February 13, 1945 | March 26, 1945 |
|--------------|--------------------|---------------------------------------|---------------------------------------|-----------------------------------|---------------------------------|---------------------------------|
| 1 | Dominants Algae | Algae | Bugula Holoporella | Bugula Holoporella | Encrusting Bryozoans | Encrusting Bryozoans |
| | Sub-dominants | Bugula | Ciona | Ciona | | |
| | Influents | Bugula | Encrusting Bryozoans Eupomatus | Encrusting Bryozoans Eupomatus | Scrupocellaria Hydroids | Scrupocellaria Hydroids |
| 2 | Dominants | Encrusting Bryozoans Eupomatus | Encrusting Bryozoans Eupomatus | Mytilus Encrusting Bryozoans | Mytilus Encrusting Bryozoans | Mytilus Encrusting Bryozoans |
| | Sub-dominants | Ciona Bugula Scrupocellaria | Ciona Bugula Mytilus | Ciona Erect Bryozoans | Erect Bryozoans | Erect Bryozoans |
| | Influents | Colonial Ascidians Mytilus Sponges | Colonial Ascidians Sponges | Colonial Ascidians | | |
| 3 | Dominants | Encrusting Bryozoans Eupomatus | Encrusting Bryozoans Eupomatus | Encrusting Bryozoans Eupomatus | Mytilus | Mytilus |
| | Sub-dominants | Ciona Bugula Scrupocellaria | Ciona Styela Scrupocellaria | Styela Mytilus | Sponges | Sponges |
| | Influents | Colonial Ascidians Mytilus Sponges | Colonial Ascidians Mytilus Sponges | Colonial Ascidians Sponges | | |
| 4 | Dominants | Encrusting Bryozoans | Mytilus Ciona | Mytilus | Mytilus | Mytilus |
| | Sub-dominants | Ciona Mytilus | Ciona | Encrusting Bryozoans | | |
| | Influents | Colonial Ascidians Erect Bryozoans | Colonial Ascidians Erect Bryozoans | | | |

tember, had a population similar to that observed on float 2 in November, with relatively large numbers of *Mytilus* and *Ciona* on a bryozoan substratum. Within a month, *Mytilus* had largely displaced the bryozoans, and within three months, *Ciona* had also disappeared.

The *Ciona* community of float 5 remained virtually unchanged from September to February. By this time, however, the *Ciona* began to show signs of deterioration. They were heavily covered with algae and hydroids, and had many small *Mytilus* about their bases. In a few places, the ascidians had fallen from the float, to be replaced by encrusting bryozoans. In March, this change had progressed so far that *Mytilus* and the bryozoans could be regarded as the dominant organisms.

Floats 6 and 7 supported two types of sponge-*Styela* communities. These were rather rapidly displaced by *Mytilus*, however. Float 8 represented a well-developed *Mytilus* community and showed no change in composition during the six months of regular observation.

These observations suggest strongly that succession is operating here. The algal community is replaced by the bryozoans, and these in turn by *Mytilus*. *Ciona* and *Styela* communities are likewise replaced by *Mytilus*, but the *Mytilus* community is relatively stable. Further information bearing on this conclusion is available from the experimental studies to be reported in the next section.

EXPERIMENTAL OBSERVATIONS WITH GLASS AND METAL SURFACES

Experimental observations were made using glass plates, and supplementary information was available from a series of aluminum panels immersed for another purpose. The fact that the changes observed on the glass plates were entirely similar to those observed on wooden floats and metal plates suggests that the changes reported here are not dependent on the nature of the submerged surface. Coe (1932) and Coe and Allen (1937) concluded that the seasonal variations in abundance of populations or of different groups of organisms were the same on glass, concrete, and wood surfaces. They did find significant differences in the numbers and types of organisms on the different surfaces, however.

The glass panels used were four by nine inch rectangles of ordinary window glass in most cases; in a few experiments three by five inch panels were used. The metal plates were five by eight inch rectangles of aircraft aluminum (Alclad ST-37). The glass panels were at first exposed in a horizontal frame (Fig. 2) of redwood weighted with concrete. The frame was suspended from the laboratory pier, situated in the entrance channel to Newport Harbor about one-half mile from the outer end of the jetties protecting the harbor entrance. A rapid tidal flow passes this point twice daily, carrying with it abundant larvae from both the quiet-water fauna of the harbor and the open shore fauna of the jetties and adjacent rocks. In the second year of this study, with the glass plates, and throughout the work with the metal plates, a vertical suspension was used to facilitate handling of larger numbers of plates. The plates were suspended in slotted redwood crates, with a distance of one inch between plates. As the growth on the plates became heavier, this distance was increased to two inches. The plates were always suspended one or two feet below the level of the lowest tides.

All of the plates were examined regularly at intervals of two weeks, and then returned to the bay. A count was made, in most instances, of the numbers of each of the larger species on one surface (always the same for any plate). An estimate was also made of the area covered by each of the more abundant types of organism. Usually, this was done by a direct count of ten or more low-power microscopic fields distributed over the surface. When a plate was finally removed from the water, the organisms were carefully removed, sorted and weighed.

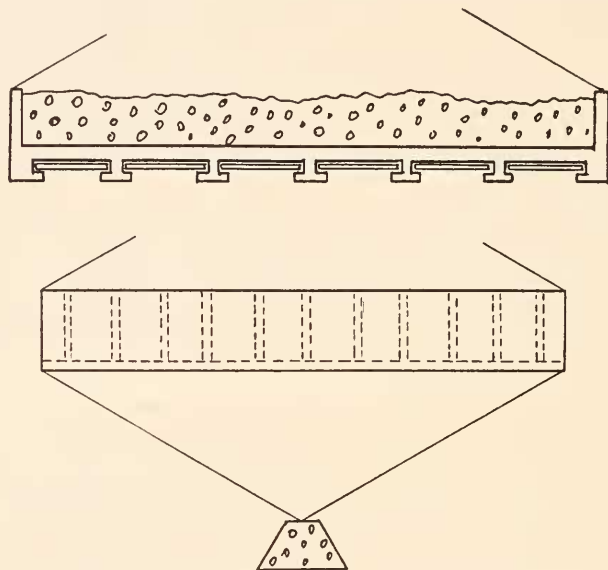


FIGURE 2. Horizontal and vertical suspension of panels.

The development of the algal community, and its transition to the bryozoan community could be followed very well on these plates. The first settlers were bacteria, diatoms, protozoans and, in the cooler months, hydroids. These were followed by the multicellular algae, especially *Ectocarpus*.

In the first months of this study it was observed that the larvae of bryozoans usually settled on the plates in quantity only after the second week of exposure, and sometimes did not settle until the fourth to sixth week. In order to verify this observation, careful counts were made during 1944 of the number of bryozoan colonies on each plate at two-week intervals. In this way, the minimum number of new settlers during any two-week period could be determined. Data obtained in this way are tabulated in Tables II, III, and IV for encrusting bryozoans, erect bryozoans and *Eupomatia*. The tabulation for the erect bryozoans omits the figures for the small semi-erect *Eucratea clavata*; representatives of this species settled in great numbers at irregular intervals, showing a behavior in this respect which was not at all comparable to the settlement of the other forms. The colonies were, moreover, rather short lived, dying often within a month of the original settlement.

During the first two weeks of exposure of any plate, the number of bryozoan and tubeworm settlements was usually less than during subsequent two-week periods. The preliminary period of light settlement was followed by a very heavy settlement in most cases. The growth of the early settlers, and in many cases, the large number of organisms settling during the maximal period, combined to reduce the available surface, and there was in consequence a very definite decrease in the number of organisms on the plate. By the time this decrease became evident, the plate was completely covered with bryozoans and tubeworms.

TABLE II
Number of new settlements of encrusting bryozoans on glass plates
during successive two-week periods, 1944

[illegible]

Figure 3 represents data derived from a metal plate first exposed March 28, 1944, and shows the changes in area covered by the algae, bacteria and hydroids on the one hand, and bryozoans on the other. The major increase in area occupied by the bryozoans occurred after the period of maximum settlement; the heaviest settlement occurred between the sixth and eighth weeks, while the rapid increase in area began between the tenth and twelfth weeks. This was in part the result of the manner of growth of bryozoan colonies. The number of new zooids formed increases directly with the number of zooids composing the colony, so that the rate of growth increases exponentially until crowding prevents further increase in the size of the colony.

TABLE III

Number of new settlements of erect bryozoans (exclusive of *Eucratea clavata*) on glass plates during successive two-week periods, 1944

| Date examined | Date of original exposure | | | | | | | | | | | | |
|------------------|---------------------------|------------|------------|------------|------------|------------|------------|----------|-----------|-----------|-----------|-------------|------------|
| | Jan. 17 | Jan. 31 | Feb. 14 | Feb. 28 | Mar. 12 | Mar. 27 | Apr. 27 | May 9 | June 8 | July 6 | Aug. 1 | Sept. 11 | Oct. 10 |
| Mar. 27 | 0 | 0 | 0 | 0 | 0 | | | | | | | | |
| Apr. 8 | 4 | 0 | 0 | 0 | 0 | 0 | | | | | | | |
| Apr. 26 | 11 | 10 | 10 | 0 | 5 | 0 | | | | | | | |
| May 9 | 20 | 20 | 28 | 35 | 48 | 3 | 0 | | | | | | |
| May 24 | 5 | 4 | 6 | — | 17 | 18 | 0 | 0 | | | | | |
| June 7 | 11 | 18 | 7 | 22 | 14 | 17 | 5 | 10 | | | | | |
| June 21 | 21 | 27 | 36 | 24 | — | 27 | 72 | 44 | 2 | | | | |
| July 6 | | | | | | | | 40 | 5 | | | | |
| July 17 | | | | | | | | | 28 | 12 | | | |
| July 31 | | | | | | | | | 33 | 3 | | | |
| Aug. 14 | | | | | | | | | 28 | 11 | 1 | | |
| Aug. 28 | | | | | | | | | | 13 | 4 | | |
| Sept. 11 | | | | | | | | | | | 9 | | |
| Sept. 25 | | | | | | | | | | | 19 | 1 | |
| Oct. 10 | | | | | | | | | | | 18 | 0 | |
| Oct. 23 | | | | | | | | | | | | | 1 |

The length of time required for this sequence of events varied with the season of the year, but the character of the sequence did not vary. Thus, the plate exposed December 20 did not reach "saturation" with encrusting bryozoans until April, while the plate exposed May 9 had become "saturated" before the end of June (Table II). If we consider any particular two-week period, however, it is

TABLE IV

Number of new settlements of *Eupomatus* on glass plates
during successive two-week periods, 1944

| Date examined | Date of original exposure | | | | | | | | | | | | | | |
|------------------|---------------------------|-----------|------------|------------|------------|------------|------------|------------|------------|----------|-----------|-----------|-----------|-------------|------------|
| | Dec. 20 | Jan. 5 | Jan. 17 | Jan. 31 | Feb. 14 | Feb. 28 | Mar. 12 | Mar. 27 | Apr. 27 | May 9 | June 8 | July 6 | Aug. 1 | Sept. 11 | Oct. 10 |
| Jan. 5 | 0 | | | | | | | | | | | | | | |
| Jan. 17 | 0 | 0 | | | | | | | | | | | | | |
| Jan. 31 | 0 | 0 | 0 | | | | | | | | | | | | |
| Feb. 14 | 2 | 0 | 0 | 0 | | | | | | | | | | | |
| Feb. 28 | 15 | 4 | 0 | 0 | 0 | | | | | | | | | | |
| Mar. 12 | 17 | 10 | 1 | 0 | 0 | 0 | | | | | | | | | |
| Mar. 27 | 7 | 1 | 6 | 2 | 0 | 0 | 0 | | | | | | | | |
| Apr. 8 | 8 | 14 | 13 | 9 | 1 | 2 | 0 | 0 | | | | | | | |
| Apr. 26 | 1 | 1 | 10 | 2 | 4 | 2 | 0 | 0 | | | | | | | |
| May 8 | 1 | 3 | 2 | — | 0 | 1 | 1 | 0 | 0 | | | | | | |
| May 24 | | | | | 2 | — | — | 0 | 0 | 0 | | | | | |
| June 7 | | | | | | | 3 | 1 | 2 | 0 | | | | | |
| June 21 | | | | | | | 0 | 3 | 0 | 7 | 8 | | | | |
| July 6 | | | | | | | 7 | 4 | 12 | 20 | 11 | | | | |
| July 17 | | | | | | | | | | | 4 | 0 | | | |
| July 31 | | | | | | | | | | | 2 | 5 | | | |
| Aug. 14 | | | | | | | | | | | — | 5 | 0 | | |
| Aug. 28 | | | | | | | | | | | 14 | 39 | 15 | | |
| Sept. 11 | | | | | | | | | | | | | 11 | | |
| Sept. 25 | | | | | | | | | | | | | — | 11 | |
| Oct. 10 | | | | | | | | | | | | | 4 | 3 | |
| Oct. 23 | | | | | | | | | | | | | | 3 | 0 |

evident from Tables II to IV, that in general, the most recently exposed plates received lighter settlements of the three types of organisms concerned than did those which had been in the water somewhat longer. Evidently changes occurred following immersion which rendered the plate more suitable for settlement of bryozoans and tubeworms than was the clean surface. These changes occurred more rapidly in the warmer months.

Two experiments were performed to test this hypothesis, and to throw more light on the nature of the changes involved. ZoBell and Allen (1935) and Coe and

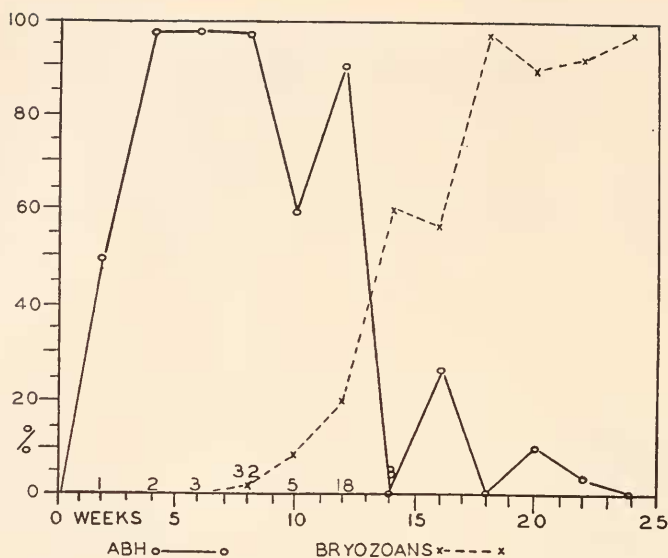


FIGURE 3. Relative areas, in per cent, covered by algae, bacteria, and hydroids (A B H), and bryozoans on an aluminum panel exposed March 28, 1944. The figures along the abscissa represent number of new settlements of bryozoans in each two-week period.

Allen (1937) have suggested that bacterial film is an important feature in the establishment of sedentary forms on a submerged surface. In the first experiment (Table V), ten three by five inch glass plates were sterilized. Two were then exposed in the bay, two were left in sterile sea water, two in a sterile solution of 0.1 per cent peptone in sea water, and two were placed in a solution of 0.1 per cent peptone in water freshly drawn from the bay. After four days, by which time a vigorous bacterial population had developed in the bay water solution, all ten

TABLE V

Settlement of organisms on pretreated glass plates, June 6-10, 1944. Duration of treatment, 4 days. Figures represent number of organisms or colonies

| Treatment: | First series (3 days immersion) | | | Second series (4 days immersion) | | |
|----------------------------------|---------------------------------|-----------|-----------|----------------------------------|-----------|-----------|
| | Hydroids | Bryozoans | Ascidians | Hydroids | Bryozoans | Ascidians |
| Sterile sea water | 43 | 0 | 0 | 68 | 4 | 0 |
| Sterile sea water + 0.1% peptone | 53 | 2 | 2 | 44 | 0 | 0 |
| Bay water + peptone (bacterial) | 150 | 2 | 2 | 174 | 4 | 0 |
| Immersion in bay 4 days | 53 | 11 | 11 | 83 | 14 | 0 |
| Sterile plate | 47 | 2 | 2 | 52 | 3 | 0 |

plates were placed in the bay. The results are presented in Table V. The hydroids evidently settled more abundantly on the bacteria-coated plates than on the others, but the bryozoans and ascidians were not influenced by the bacterial coating. Rather, they settled more abundantly on the plates which had been in the bay longest; these plates had a more abundant diatom population than did the others.

A second similar experiment was carried out in the fall, with daily observations during several weeks of exposure, and careful determinations of the bacterial and algal populations. Diatoms appeared on the plates in small numbers within the first two to four days in the bay (Table VI). For a period of two to three weeks, however, the diatoms covered less than 5 per cent of the surface. This period was

TABLE VI

Settlement of organisms on treated panels, October 21 to November 24, 1944. The figures represent the per cent of the area of one side of the panel covered by bacteria, diatoms, and protozoans respectively, and total number of organisms or colonies on one side of the panel for the larger organisms (bryozoans, annelids, ascidians).

| Duration of treatment: | | 5 days | | | | 18 days | | | |
|-------------------------------------------------------|----------------------------------------|--------|---------|-----------------------------|---------------------------|---------|---------|-----------------------------|---------------------------|
| Treatment: | | Bay | Sterile | Sterile sea water + peptone | Fresh bay water + peptone | Bay | Sterile | Sterile sea water + peptone | Fresh bay water + peptone |
| Days after treatment | Organism | | | | | | | | |
| 7 | Bacteria | 0.3% | 0.2% | 0.3% | 1% | | | | |
| | Diatoms | 4% | 1% | 1% | 1% | 80% | 1% | 2% | 11% |
| | Protozoans | + | + | + | + | | 0.3% | 1% | 1% |
| | Bryozoans: | | | | | | | | |
| | Membranipora | 6 | 3 | 1 | 9 | 0 | 1 | 0 | 0 |
| | Other encrusting forms | 0 | 0 | 2 | 0 | 8 | 1 | 2 | 3 |
| | Annelids | 0 | 1 | 0 | 3 | 3 | 0 | 0 | 8 |
| | Ascidians | 1 | 0 | 5 | 3 | 0 | 0 | 3 | 7 |
| 16 | Bacteria | 1% | 1% | 2% | 1% | | | | |
| | Diatoms | 35% | 11% | 8% | 16% | 51% | 5% | 7% | 8% |
| | Protozoans | 6% | 1% | 0.1% | 6% | | 5% | 4% | 18% |
| | Encrusting bryozoans exc. | 13 | 6 | 11 | 14 | 14 | 3% | 5% | 6% |
| | Membranipora | | | | | | | | |
| | Annelids | 1 | 2 | 2 | 3 | 8 | 0 | 1 | 9 |
| | Ascidians | 2 | 2 | 9 | 5 | 0 | 2 | 1 | 0 |
| Time of maximum increase, days after immersion in bay | Diatoms | 19 | 14 | 20 | 14 | 19 | 16 | 14 | 16 |
| | Encrusting bryozoans exc. Membranipora | 19 | 14 | 22 | 16 | 21 | 16 | 16 | 16 |

followed by a relatively sudden increase in the number of diatoms, until 25 per cent to 80 per cent of the plate was covered. The reason for this delay is not clear. During the first two to three weeks of exposure, bacteria and protozoans as well as diatoms settled on the plates. That bacteria were not concerned in the eventual diatom outburst is indicated by the fact that the bacteria-coated plates (bay water and peptone) showed no difference from the other plate in the time of the outburst. About 5 per cent of the area of the plate which had been immersed in bay water plus peptone for five days was covered with bacteria when the plate was immersed in the bay; the eighteen day plate was covered to an extent of about 11 per cent. This coating was largely lost within a few days, however. It is noteworthy that, although the time of maximum increase of the diatoms was not affected by the presence of bacteria, larger populations of diatoms eventually developed on the bacteria-coated plates than on the other plates. Algae other than diatoms were not important in this experiment; *Ectocarpus*, *Enteromorpha*, *Cladophora*, *Scytosiphon*, *Pterosiphonia* and *Lophosiphonia* were noted, but did not appear in quantity until some time after the diatom increase.

The data available from this study are not sufficient to establish a succession within the algal community. Wilson (1925), however, has reported a definite sequence, involving diatoms, hydroids and filamentous algae, on rocks at La Jolla. It is quite possible that careful study over a longer period would reveal a similar situation here.

It appears that the relatively heavy growth of diatoms on the bay water plus peptone plates is correlated with a correspondingly heavy settlement of bryozoans. Whether there is a direct causal relation between diatom growth and bryozoan settlement is uncertain. However, the maximum period of bryozoan settlement never preceded, and usually followed, the period of maximum diatom increase in the experiment of Table IV.

The encrusting bryozoan *Membranipora tuberculata*, which normally inhabits the stipes of kelp, occurred on the experimental plates only on one occasion, and remained only a short time. Most of the colonies fell from the plate within the space of a month. Unlike the other bryozoans, however, this species showed definite preference for the bacteria-coated plate.

These experiments suggest, then, that the important change which occurs on plates favoring bryozoan settlement, is the growth of diatoms. In view of this conclusion and of the fact that the bryozoan community, throughout the course of this study, has been observed to form only on surfaces previously supporting an algal growth, we may say that a definite succession is established.

The observations on the glass plates provide little evidence concerning the other communities, but two instances are worthy of mention. The development of a *Styela* community from a bryozoan community was noted in one instance, on a plate exposed horizontally in March 1943. The algal coat which developed upon exposure was displaced by bryozoans before the end of June. In September, however, specimens of *Styela* which had settled in July had become so large as to dominate the community. The remaining bryozoans gradually lost ground and fell from the plate, leaving *Styela* as the principal organism present. The fact that *Styela* was always found growing out of a substratum of old bryozoan colonies on the floats examined in the course of this study indicates that this sequence probably occurs frequently.

The second instance concerns the formation of a *Balanus* community. The plate concerned was exposed horizontally in August 1943. The algal community formed very rapidly, and in addition, within two weeks, larvae of *Eupomatus*, encrusting bryozoans, *Pecten* and *Balanus* had settled in large numbers. In the ensuing competition for space, the barnacles emerged victorious. In September, there were more than two hundred barnacles on the exposed side of the plate, covering the surface almost completely. An equal number of *Eupomatus* occupied the spaces between the barnacles, but encrusting bryozoans were not abundant. During subsequent months, however, growth of the bryozoans was continuous, and by December, the barnacles were almost completely covered by the rapidly growing bryozoans.

DISCUSSION AND CONCLUSIONS

In order to make a satisfactory analysis of the phenomena described in the preceding sections, it would be necessary to know (a) the breeding seasons of the organisms involved, (b) the normal duration of life of each of the important organisms, (c) the length of the free-swimming larval period in each case, and (d) the nature of the surfaces to which such free-swimming larvae will attach. We do not have such information in most cases. Nevertheless, it is possible to make some interpretations on the basis of the available information.

It was stated at the outset that the basic problem is that of distinguishing between seasonal progression and true succession. Several examples of progression were noted at Beaufort, N. C. by McDougall (1943). The organisms which settled during the winter were, for the most part, dead or moribund by spring, and were consequently replaced by organisms breeding chiefly in the spring. There is some reason to expect that seasonal progression may be less important in Newport Harbor than at Beaufort. The annual range of monthly mean temperatures at Beaufort is 23° C., from 5.5° in February to 28° in July. The annual range in Newport Harbor is only 5° C., from a low of 14.1° in February to a high of 19.2° in July. The breeding seasons of most of the organisms involved in the sequences described here extend through most of the year. Certainly algae, bryozoans and mussels have been observed to settle during every month of the two years covered by this study.

In the present study, it seems probable that the algal community, and most probably the diatoms comprising the basis of that community, provide favorable conditions for the settlement of bryozoans. Bryozoans settled in quantity only after the development of a fairly vigorous algal community. Moreover, in the experimental test described in Table VI, bryozoan settlement was definitely correlated with the settlement and growth of diatoms. There remains the possibility that some common factor favored settlement of both diatoms and bryozoans, the former remaining "dominant" only until the slower but persistent growth of the latter displaced them. It is difficult to rule out such common factors, but it appears unlikely that chemical alterations in the glass on exposure to sea water are involved. The plates used in this particular experiment had previously been immersed in the bay for two months. They were then scrubbed with a brush in tap water, wrapped in paper and sterilized in an autoclave. The experimental plates were soaked in three liters of solution for several days as noted in the table,

TABLE VII

Weights of organisms removed from glass and aluminum panels, 1943-44
(+ sign indicates organisms present in amounts of less than 1 gram)

| Surface: | Glass | | | | | | | | | | | | | | | | Aluminum | | G | G | Al |
|------------------------------------|------------------|------------|-------------|-------------|-----------|------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|--------------|-------------|-------------|-------------|-------------|---|---|----|
| | 4 | | | 8 | | | 12 | | | 20 | | | 26 | 28 | 32 | 36 | | | | | |
| Duration of exposure, weeks: | Mar. 12 '43 | Apr. 4 '43 | Dec. 20 '43 | Mar. 12 '43 | May 7 '43 | July 5 '43 | Dec. 20 '43 | Dec. 20 '43 | Dec. 20 '43 | Jan. 31 '44 | Feb. 28 '44 | Mar. 27 '44 | Apr. 27 '44 | Sept. 21 '43 | Mar. 28 '44 | Jan. 17 '44 | Dec. 20 '43 | Dec. 14 '43 | | | |
| Date of initial exposure: | 12 '43 | 4 '43 | 20 '43 | 12 '43 | 7 '43 | 5 '43 | 20 '43 | 20 '43 | 20 '43 | 31 '44 | 28 '44 | 27 '44 | 27 '44 | 21 '43 | 28 '44 | 17 '44 | 20 '43 | 14 '43 | | | |
| Total weight of organisms, grams: | 20 | 56 | 9 | 23 | 67 | 18 | 12 | 19 | 117 | 204 | 302 | 174 | 157 | 83 | 194 | 193 | 180 | 128 | | | |
| Per cent of weight contributed by: | | | | | | | | | | | | | | | | | | | | | |
| Algae, Bacteria, Hydroids, Debris: | 100 | 85 | 100 | 87 | 76 | 28 | 100 | 81 | 2 | 1 | 30 | 9 | 29 | 59 | 21 | 18 | 15 | 11 | | | |
| Bryozoans | Encrusting forms | | | | | | | | | | | | | | | | | | | | |
| | Erect forms | | | + | 9 | 3 | + | + | 21 | 22 | 11 | 25 | 16 | 2 | 6 | 28 | 17 | 1 | | | |
| Annelids | Serpulids | | | | + | 14 | + | + | 10 | 2 | 1 | + | 3 | 6 | 1 | 5 | 8 | 1 | | | |
| | Others | | 8 | + | 1 | | + | 3 | 1 | 5 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | | | |
| Crustaceans | Erichthonius | | 4 | + | | 3 | + | 11 | 8 | 5 | 21 | 14 | 6 | 1 | 3 | 10 | 19 | 5 | | | |
| | Balanus | | | | | 14 | | | + | | + | + | + | 1 | + | | | 1 | | | |
| | Others | | 3 | + | 1 | 3 | + | + | | + | + | + | + | + | | + | + | + | | | |
| | Pecten | | | + | 10 | 6 | + | | | | | + | 1 | | + | + | + | + | | | |
| Mollusks | Mytilus | | | | | | | | | | | | | | 3 | | | | | | |
| | Saxicava | | | + | + | | | | + | + | + | + | 2 | + | 1 | 8 | 4 | 8 | | | |
| Sponges | | | | | | | | | | 5 | + | | | 1 | + | + | + | + | | | |
| Ascidians | | + | | + | | + | | | 1 | 5 | 1 | 11 | 1 | | 1 | 2 | 2 | 5 | | | |

while the control plates were placed directly in the bay. The same sequence of organisms is apparent on both experimental and control plates, and the periods of time involved are not significantly different.

The data in Table VII are of interest in this connection. It is apparent that the organisms listed fall into four classes: (1) Those which appear in abundance on all plates, but most abundantly on those exposed for the shortest periods (algae, etc.). (2) Those which appear only on plates exposed more than four weeks, and most abundantly on plates exposed twenty weeks or longer (bryozoans, serpulid worms). (3) Those which appear in measurable quantities only on plates exposed twenty weeks or longer, and are not abundant even on plates exposed as long as thirty-six weeks (*Mytilus*, *Saxicava*, sponges, ascidians). (4) Those which appear irregularly, without relation to the duration of exposure (annelids, *Balanus*, *Erichthonius* and other crustaceans, *Pecten*).

It is particularly significant that the dominant organisms of the primary communities involved in the sequence described earlier—viz. algae, bryozoans, ascidians and mussels—fall into separate categories on this basis, and that the sequence here is the same as that observed in the sequence of communities. It appears that the settlement of ascidians certainly and mussels probably is favored by the existence of a thriving bryozoan community.

In any event, there is no evidence that seasonal progression is involved to a significant extent in the algae-bryozoan-*Mytilus* sequence. A plate exposed in December went through the same sequence as did one exposed in March or April; the time relations varied, but the sequence did not. And in the absence of a seasonal progression, it is difficult to avoid the conclusion that true succession is involved.

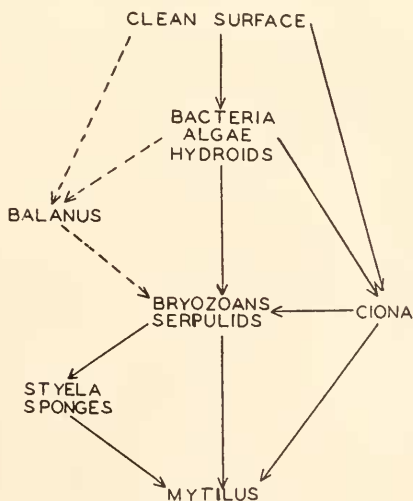


FIGURE 4. Sequence of dominant organisms on surfaces exposed in Newport Harbor.

In many studies of the life histories of sedentary organisms, estimates of the season of settling have been based on the number of new settlers on a plate exposed for a brief period. It is evident from the results reported here that such

estimates may be unreliable if succession is involved in the settlements under consideration. Thus, plates exposed for four weeks or less in Newport Harbor in the winter months would receive few or no settlements of bryozoans, despite the fact that settling larvae are present in the water during these months. It is important, therefore, that studies of this sort take into consideration the question whether succession is occurring.

With the evidence presented in this paper, we can make a number of suggestions as to the possible factors involved in the events described. The sequence is depicted in Figure 4. A newly exposed surface is first colonized by bacteria, algae and, in some seasons, hydroids. The development of these forms provides a favorable surface for establishment of bryozoan colonies, and also for the settlement of serpulid larvae. The vigorous growth of the bryozoans eventually displaces the algae and hydroids. The resulting bryozoan community in turn provides a favorable basis for the attachment of *Mytilus* larvae. The growth of the mussels effectively covers the whole surface of the bryozoan community, the members of which eventually perish from lack of food, oxygen, etc. Seasonal factors, involving the settlement of ascidian or barnacle larvae in tremendous numbers, may introduce variations into this sequence. *Ciona* may sometimes colonize a clean surface, or one covered with algae, to such an extent that the bryozoans are unable to maintain their foothold. *Styela* apparently settles only on bryozoan substrata, but may become established before *Mytilus*, and hence a community dominated by *Styela* may follow the bryozoan stage. Sponges are frequently associated with *Styela*. Both *Ciona* and *Styela* communities are eventually displaced by *Mytilus* which at present represents the climax in the float-bottom associations of Newport Harbor.

SUMMARY

1. The sedentary communities characteristic of float bottoms in Newport Harbor, California, are described.
2. The most important communities at present are dominated, respectively, by algae, bryozoans, *Ciona intestinalis*, *Styela* sp. and *Mytilus* sp.
3. These communities represent stages in an ecological succession.
4. The algal community appears first on freshly exposed surfaces, to be followed usually by a bryozoan community.
5. The bryozoans prominent in the bryozoan community settle more readily on surfaces supporting a vigorous growth of diatoms and other algae than on clean surfaces.
6. The community dominated by *Mytilus* constitutes the climax at present.
7. *Mytilus* has been observed to settle only on surfaces bearing a bryozoan, *Ciona* or *Styela* community.
8. The establishment of *Ciona* or *Styela* communities appears to depend in part on seasonal factors.

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